



Allometric Relationships in Field-grown Soybean

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Allometric relationships in plants uncover size-correlated variations in form and development and characterize the relative growth of a part of a plant in comparison with a whole. Stable allometric relationships in ontogeny can be used as components of crop models and to estimate plant parameters that are difficult to measure. Our objective was to discover whether stable allometric relations exist in ontogeny of field-grown soybeans (*Glycine max* L.). We used field data on vegetative stages, plant height, stem weight, and leaf weight of 16 soybean cultivars measured on farms and on the experiment station of Mississippi State University during 1993–1995 growing seasons. The number of observed crops for each cultivar ranged from one to 14. Stem heights displayed linear log-log dependencies on the vegetative stage, before and after the breakpoint stage, which typically was between the 'fourth node' and 'sixth node' vegetative stages. Slopes of the log-log dependencies after the breakpoint stage were similar in all cultivars. Stem mass had log-log linear dependencies on stem height. Slopes of these dependencies differed among cultivars grown under the same conditions, and among crops of the same cultivar grown under different conditions. Water stress could be a modifier of these relationships. The proportion of leaf weights in the total weight of leaves and stems decreased linearly as the vegetative development progressed. Since allometric relations are stable for a specific crop, they can be used to forecast vegetative development as soon as they are established. © 1998 Annals of Botany Company

Key words: Soybean, *Glycine max* L., allometry, vegetative development.

INTRODUCTION

Plant allometry studies aim to uncover size-correlated variations in organic form and process (Huxley, 1932). Allometry is also used to study and measure relative growth of part of an organism, in comparison with the whole (New Webster Dictionary, 1989). Allometric relations have been found in a broad variety of plant species, and are viewed as the consequence of natural selection and adaptive evolutionary changes (Niklas, 1994). Allometric relations can be developed from ontogenetic comparisons, and from intraspecific and interspecific comparisons. Examples of allometric relations discussed in the literature include relationships between height and stem mass, between height and stem diameter, between fruit and seed mass, between developmental rates of different organs, and between growth rate and cell biomass.

Allometric relations from intraspecific comparisons are often based on data from mature plants (Gould, 1966; Niklas, 1994). Such relationships can be used to estimate plant parameters that are difficult to measure, such as total plant biomass or root mass. Most examples are related to trees (Whitaker and Woodwell, 1968; Ek, 1979; West, Beadle and Turnbull, 1989), although successful results have also been reported for potato crops (Moorby, 1967; Plaisted, 1967) and for barley crops (Hamid and Grafius,

1978). Observations of ontogeny have also resulted in the discovery of stable allometric relationships between time-dependent plant parameters. These relationships find applications in modelling plant growth, estimating growth rates of specific organs from growth rates of other organs, or the plant as whole (Pešek, 1976).

Allometric relations have often been treated as genetically fixed characteristics of plant species (Weller, 1987) or as features of a group of species (Niklas, 1995). Allometric differences would be expected between cultivars of the same plant. It has been shown that genetic modifications in wheat lead to changes in ontogenetic allometry (Lenton, Heddon and Gale, 1987). Modern studies suggest that the ability of plants to adapt to the environment can affect allometric relationships, especially in annual plants (Reekie and Bazzaz, 1987; Marvel, Beyrouthy and Gbur, 1992; Weiner and Thomas, 1992). Allometric parameters such as the harvest index, defined as a ratio of the seed mass to the above-ground biomass, vary over broad range, and depend on growing conditions (Mayers, Lawn and Byth, 1991; Prior and Rogers, 1995).

Knowledge of ontogenetic allometric relationships in agricultural plants is important, both in developing crop simulators, and in estimating crop parameters from remote sensing data. Using easily measurable plant parameters, such as vegetative stage or height, to estimate dry mass of plant organs can provide data required to estimate carbon accumulation rates and water and nutrient requirements. Including stable allometric relationships in crop simulators

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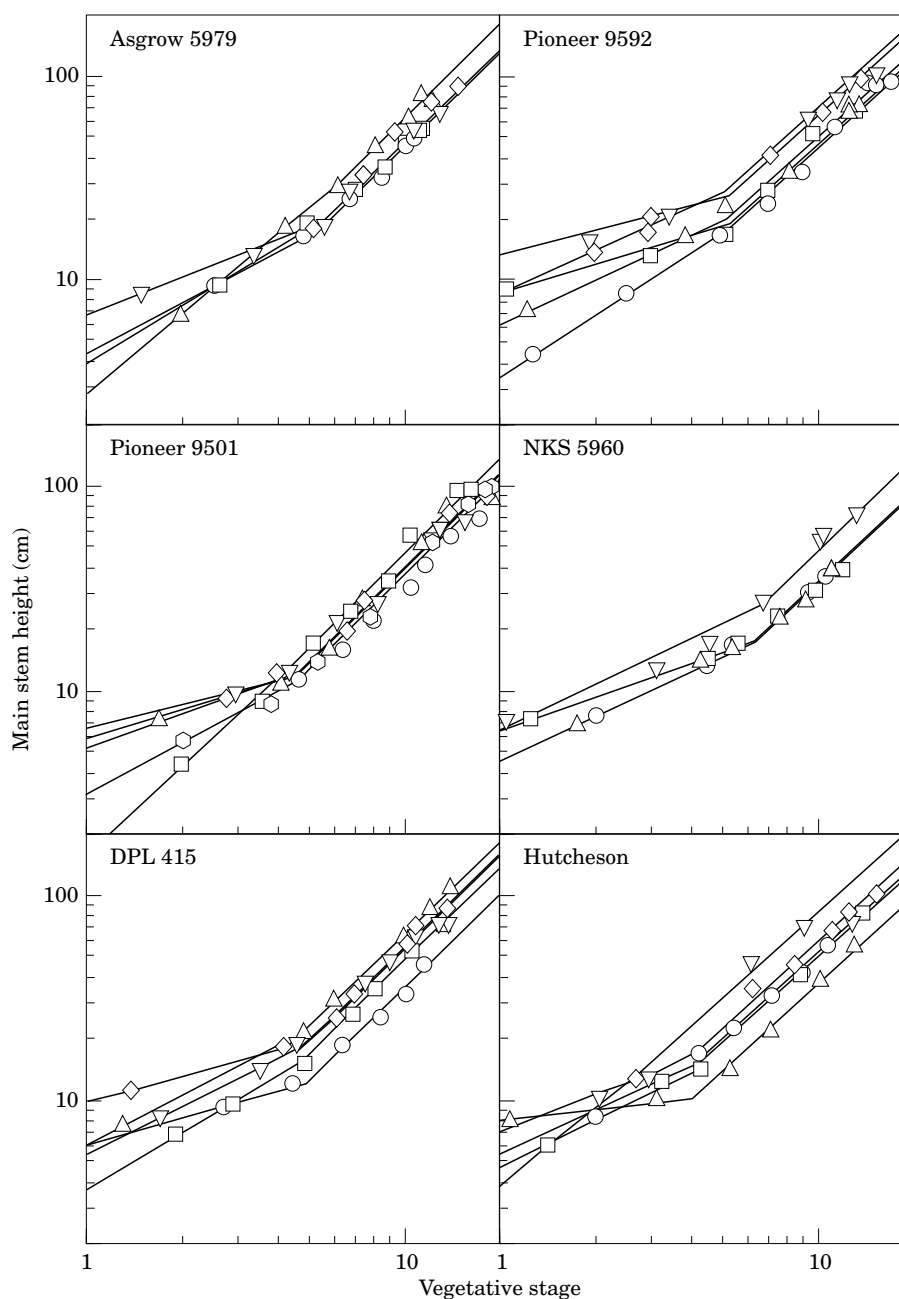


FIG. 1. Relationships between main stem height and vegetative stages in crops of six soybean cultivars. See Table 1 for explanation of symbols.

increases their reliability, and this is crucial when the simulators are used as management tools for crop management and input optimization in farming.

We tested the soybean crop simulator GLYCIM as an advisory tool in the Southern United States, and found a need for improvement in its predictions (Reddy *et al.*, 1995). One possibility was to investigate the use of ontogenetic allometric relations in the simulator. Our objective was to discover whether stable allometric relations exist in ontogeny of field-grown soybeans, limiting our study by using data on vegetative development only.

MATERIALS AND METHODS

Data on vegetative development of soybeans were collected from farms in the lower Mississippi Valley area during 1993–1995, and from the experimental fields of the Mississippi State University in 1994. The number of crops for each cultivar ranged from one to 14. Vegetative stages, main stem height, stem dry mass, dry mass of branches, and dry leaf mass were measured for 20 plants from five sites within each field, nine–13 times during growing seasons. Vegetative stages of soybean plants were defined as

suggested by Fehr and Caviness (1977). The vegetative stage of each plant was represented by the number of nodes on the main stem with fully developed leaves, beginning with the unifoliate nodes. The vegetative stages are labelled numerically so that V1 corresponds to the first fully developed node, V2 corresponds to the second fully developed node, and so on.

To define the vegetative stage of a crop, we assumed that it can be a fractional number, equal to the average of the integer vegetative stages of 20 sampled plants. For example, if 14 plants were at V3 stage, four plants were at V2 stage and two were at V4 stage, then the vegetative stage of the crop V was $(4 \times 2 + 14 \times 3 + 2 \times 4)/20 = 2.9$.

Soil sampling was carried out between growing seasons. Weather records included daily minimum and maximum temperatures, solar radiation, rainfall, and wind run, which were collected from meteorological stations located in the fields. Farmers' irrigation records were used to find the total water supply to crops.

Three ontogenetic allometric relations were studied. A relationship between the relative increment of the main stem height (H) and the relative increment of the vegetative stage of the crop (V) was assumed in the form:

$$\frac{dH}{H} = \beta \frac{dV}{V} \quad (1)$$

Integration of this equation to obtain height as a function of the vegetative stage gives:

$$\log H = \alpha + \beta \log V \quad (2)$$

where β is a scaling exponent and α is a scaling coefficient (Niklas, 1994). The logarithm base 10 is used here and below.

A relationship between the relative increment of the main stem dry mass M and the relative increment of the main stem height H was assumed in the form:

$$\frac{dM}{M} = \mu \frac{dH}{H} \quad (3)$$

Integration of this equation to obtain stem biomass as a function of height gives:

$$\log M = \nu + \mu \log H \quad (4)$$

where μ is a scaling exponent and ν is a scaling coefficient (Niklas, 1994).

The third allometric relationship studied was that between the increment of the proportion of leaf mass in total shoot mass F_L and increment of the crop vegetative stage V . The equation used was:

$$dF_L = -\gamma dV \quad (5)$$

Integration of this equation to obtain the proportion of leaf mass in the shoot mass as a function of the crop vegetative stage gives:

$$F_L = \delta - \gamma V \quad (6)$$

where γ is a scaling exponent and δ is a scaling coefficient (Niklas, 1994).

To find the scaling exponents and coefficients, we fitted eqns (2), (4) and (6) to data on each cultivar. Inspection

of dependencies of $\log H$ on $\log V$ (Fig. 1) has shown that height usually has two intervals of growth with distinctly different rates. To describe this type of allometric behaviour, we used equation (2) in each of the intervals:

$$\log H = \begin{cases} \alpha + \beta_1 \log(V - \log V_*), & V < V_* \\ \alpha + \beta_2 (\log V - \log V_*), & V \geq V_* \end{cases} \quad (7)$$

where V_* is termed 'breakpoint' stage and denotes the vegetative stage when the slope of the $\log H - \log V$ relationship changes. Parameters $\alpha, \beta_1, \beta_2, V_*$ of the piecewise linear dependence (7) were found by fitting this equation to data. To do this, we used a version of the Marquardt-Levenberg algorithm (Van Genuchten, 1981) which enabled us to obtain parameter values that minimized mean square model error, and to estimate the s.e. of the parameters. Having the s.e. of the parameters available, we could test for significant differences between parameter values.

The difference between accumulated precipitation and cumulative potential transpiration, or a potential water deficit, was used as an index of the water stress. A potential transpiration rate was calculated from daily values of solar radiation, maximum and minimum temperature, and the wind run, using a modified Penman-Monteith equation and downscaling of daily weather parameters to hourly level, as reported by Acock and Trent (1991).

RESULTS AND DISCUSSION

Table 1 summarizes the growth conditions used to examine ontogenetic allometric relations between main stem height H and vegetative stage V in crops. These data consist of a range of emergence days, soil textures, and plant densities typical of soybean production in the lower Mississippi Valley.

Logarithmically transformed data on ' H -on- V ' dependencies are shown in Fig. 1. Most of the dependencies have two intervals of linearity. Slopes β_1 of dependencies vary significantly from one crop to another at early stages of the vegetative development. Starting from the breakpoint vegetative stage V_* about V4-V6, slopes of $\log H - \log V$ dependencies tend to be very close for crops of the same variety. Distinctly different scaling intervals in ontogenetic allometric relationships were observed by other authors, for example, by Engel and Rauber (1962) in potato plants.

Assuming that the breakpoint vegetative stage V_* and slope β_2 are cultivar-specific, and slopes β_1 reflect growth conditions, we found parameters V_* and β_2 for each cultivar. Results are shown in Table 2, and graphs of the corresponding piecewise dependencies are seen in Fig. 1. Neither slopes β_2 nor breakpoint vegetative stage V_* were different among the cultivars. The average V_* over all six cultivars was 5.1 and the average β_2 was 1.5. Therefore, the dependence of the plant height on the vegetative stage after V5 can be approximated as:

$$\frac{H}{H_*} = \frac{V}{5}^{1.5} \quad (8)$$

where H_* is the height reached at V5. We conjecture that this dependence may be related to mechanical design of the

TABLE 1. Soybean cultivars and growing conditions of crops used to develop the allometric relationships shown in Fig. 1

Symbol in Fig. 1	Emergence date	Soil, texture	Population density (plants m ⁻²)
Asgrow 5979, Maturity Group V			
○	26 May 1993	Sharkey silty clay loam	38.7
□	26 May 1993	Dubbs sandy loam	33.7
△	22 May 1994	Sharkey clay	43.4
▽	10 May 1994	Marrietta loam	22.4
◇	20 Jun. 1996	Adler silt loam	33.6
Pioneer 9592, Maturity Group V			
○	22 May 1994	Forestdale clay loam	20.7
□	10 May 1994	Marrietta loam	23.7
△	10 May 1995	Sharkey clay	25.8
▽	24 Jun. 1995	Commerce silt loam	109
◇	24 Jun. 1995†	Commerce silt loam	107
Pioneer 9501, Maturity Group IV			
○	17 May 1993	Dundee sandy loam	25.8
□	13 May 1994	Dundee sandy loam	23.2
△	6 May 1994	Marrietta loam	26.3
▽	20 May 1995†	Bosket sandy loam	24.5
◇	20 May 1995	Dundee silty clay loam	23.2
	23 May 1995	Sharkey clay	15
NKS 5960, Maturity Group V			
○	10 Jun. 1993	Dundee loam	35.5
□	10 Jun. 1993	Sharkey silty clay loam	35.5
△	10 Jun. 1993	Forestdale clay loam	35.5
▽	10 May 1995	Sharkey clay	27.7
DPL 415, Maturity Group V			
○	24 Jun. 1993	Sharkey silty clay	25
□	10 May 1994	Sharkey silty clay	21.5
△	10 May 1995	Abernathy silt loam	20.7
▽	4 Jun. 1995	Sharkey silty clay	32.7
◇	22 May 1995†	Memphis silt loam	60.9
Hutcheson, Maturity Group V			
○	2 Jun. 1993	Sharkey silty clay loam	38.3
□	23 May 1994	Dundee silt loam	24.8
△	10 May 1994	Marrietta loam	25
▽	7 Jun. 1995	Sharkey silty clay loam	36
◇	4 Jun. 1995	Dundee silt loam	34.2

† Unirrigated crop.

TABLE 2. Parameters of allometry in soybean growth: slope (β_2) of the logarithmic dependence of height on the vegetative stage, and the break-point vegetative stage (V_*) at which this log-linear dependence begins

Cultivar	β_2	V_*
Asgrow 5979	1.53 ± 0.06†	5.67 ± 1.06
Pioneer 9592	1.43 ± 0.12	5.26 ± 1.14
Pioneer 9501	1.54 ± 0.06	4.62 ± 1.10
NKS 5960	1.48 ± 0.10	6.39 ± 1.08
DPL 415	1.52 ± 0.04	4.94 ± 1.05
Hutcheson	1.42 ± 0.05	3.99 ± 1.08

† s.e. follows '±' sign.

soybean plant, intended to carry a fruit load at a later stage of development. The allometric relationships for these traits may be very different in the winy phenotypes from which these cultivars were selected. Plant breeders, when selecting

phenotypes capable of standing erect to maturity, may have inadvertently selected for such mechanical design, and thus the allometric relation. For these, or other reasons as yet undiscovered, in all current high-yielding cultivars we studied, the ontogenetic allometric relation between H and V continues for the whole period of vegetative development after V_5 .

Development before the breakpoint vegetative stage V_* seems to be affected by growth conditions. Within data on the same cultivar, crops with the earliest emergence date usually show the minimal slope β_1 . These crops do not alter significantly in height after emergence, until the breakpoint vegetative stage is reached. A comprehensive study is needed to discover which environmental variables govern relationships between height and vegetative stage before V_4 – V_5 .

The relationships between mass (M) and height (H) of the main stem are shown in Fig. 2. This figure demonstrates stable allometric 'M-on-H' dependencies in ontogeny. These dependencies follow eqn (4). Scaling exponents μ are shown in Table 3.

We hypothesize that the decrease in the scaling exponent may reflect a structural response of soybean plants to an unfavourable growth condition. The potential water deficit in crops, seen in Fig. 2, is characterized in Fig. 3. Comparison of data in Figs 2 and 3 shows that, in all cultivars, the exponent μ exhibits dependence on the potential water deficit. Differences between estimates of μ are statistically significant for only one cultivar out of four. However, in all cultivars, the higher the potential water deficit, the lower the scaling exponent μ . Assuming that the potential water deficit correlates with the actual water deficit, we found that plants grown under a water deficit showed less relative increase in stem mass per unit relative increase in height than plants that do not experience a water deficit. Assuming the same density of the stem tissue in all plants, we concluded that relative increase in stem radius per unit relative increase in height is lower in stressed plants, i.e. soybean plants under stress had thinner stems, and plants under stress were taller for the same stem mass. Similar responses of soybean plants to stresses have been observed elsewhere. For example, Marvel *et al.* (1992) considered the ratio of plant height to stem circumference as an index of structural response of the soybean plant to competition due to plant density. In this study, this ratio decreased as the level of competition increased. Teramura and Sullivan (1987) studied the inhibiting effect of UB-B on soybean plants. Their data showed that an increase in stress decreases the scaling exponent, in relation to plant height and plant dry weight. The effect of the population density-related stress on the stem mass *vs.* stem height scaling was observed for annual plants (Weiner and Thomas, 1992), and for trees grown in different density stands (Niklas, 1994). However, such an effect may not manifest itself if differences in plant density do not cause variations in stress level (West *et al.*, 1989).

Scaling exponents were significantly different among four cultivars grown in the same environment and under the same management, in 1994 on Marietta loam soil, with a low water deficit (Fig. 2, Table 3). The allometric relation-

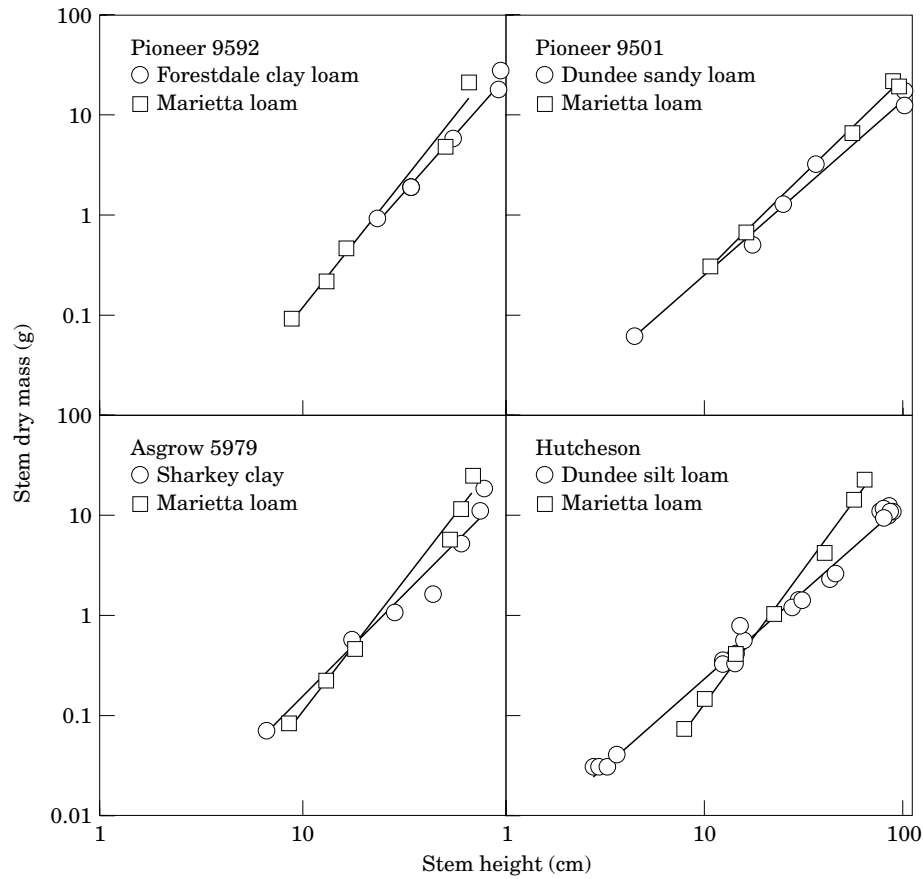


FIG. 2. Relationships between height and dry mass of main stem in crops of four soybean cultivars.

TABLE 3. Slope of the log-log relationships between the main stem dry mass and height

Cultivar	Level of potential water deficit	
	Moderate	Low
Pioneer 9592	$2.32 \pm 0.14^\dagger$	2.53 ± 0.18
Pioneer 9501	1.80 ± 0.09	1.98 ± 0.06
Asgrow 5979	2.07 ± 0.19	2.57 ± 0.15
Hutcheson	1.77 ± 0.03	2.71 ± 0.09

† s.e. follows ' \pm ' sign.

ships between main stem mass and main stem height were stable for each crop in its ontogeny, but appeared to be cultivar-specific.

Data on proportion of leaf weight in the total shoot weight F_L are shown in Fig. 4. Dependence of F_L on the vegetative stage V was similar for all 11 crops. This dependence could be approximated using the straight line from eqn. (6) in the range of V between 2 and 12, where the slope γ is equal 0.029, and r^2 is 0.89. Growing conditions did not appear to affect this dependence.

The allometric relationships studied here need to be researched further, in the context of a general biological problem of plant allometry. Biomechanical principles, structure of the canopy, carbon allocation among organs

during vegetative development, and other factors, were found to be essential for explaining allometric relationships (Niklas, 1995; Sugiyama, 1995; Yokozawa and Hara, 1995). The factor or factors governing ontogenetic allometry of soybeans remain to be discovered. The allometry shown in this paper invites research into other allometric relations in soybeans, such as allometry of nitrogen accumulation, which has been found in stressed cotton plants and cowpea (Hibberd *et al.*, 1995; Sadras and Wilson, 1997); allometry of self-thinning which has been shown in *Medicago sativa* L., *Lolium perenne* L., and in *Ocimum basilicum* L. (Morris and Myerscough, 1991; Matthew *et al.*, 1995); and allometry of plant variation in carrot populations (Li, Watkinson and Hara, 1996). The discovery of such relationships could help quantify and explain the effect of plant population density on growth and development of soybean crops. The change in the 'height-vegetative stage' relationship at the breakpoint stage is an example of multiphasic allometry (Koops and Grossman, 1993). The factors affecting this relationship at the early development stage need to be investigated in order for this relationship to be used in soybean crop simulators.

It will be possible to use stable ontogenetic relations in a specific crop to forecast its vegetative development, when scaling exponents and scaling coefficients are developed early in the growing season. We recognize that the results of this study are limited by the temporal and spatial scales of

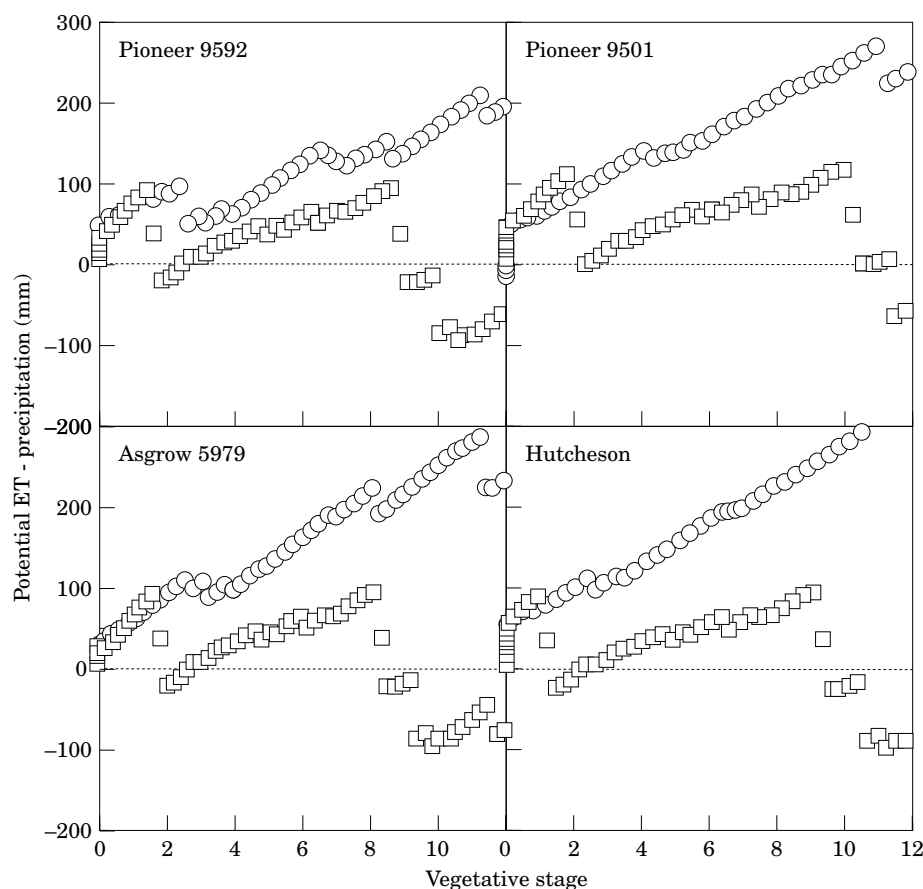


FIG. 3. Difference between precipitation and potential evapotranspiration during vegetative development of soybean crops. Symbols as in Fig. 2.

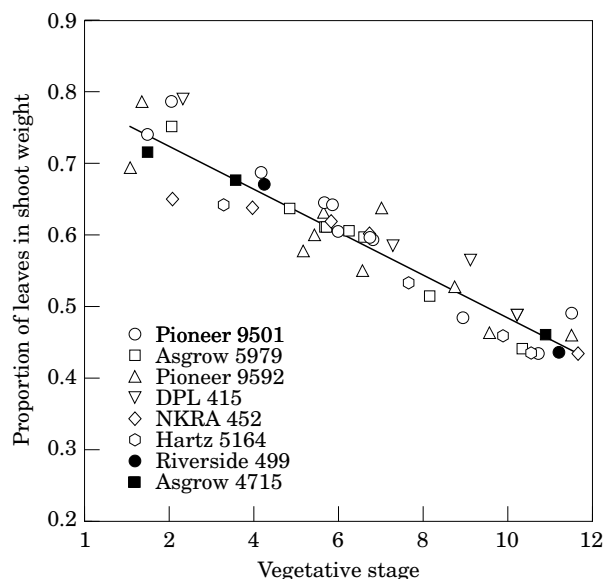


FIG. 4. Proportion of leaf mass in the shoot mass during vegetative development.

our observations. The incidence of allometric relations in soybean crops, and how and why growth conditions affect ontogenetic allometry in soybeans, are still not known, and represent exciting horizons to explore.

CONCLUSIONS

Allometric relations between height and vegetative stage, between stem height and stem mass, and between proportion of leaves in the total shoot mass and vegetative stage are stable in ontogeny of each crop that we have observed. However, these relations can vary between crops of the same soybean cultivar grown in different environments. More studies are needed in order to understand how and why growth conditions affect ontogenetic allometry in soybeans.

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